


GROWTH RESPONSE OF LUTZ SPRUCE SAPLINGS TO THE REMOVAL OF A
HERBACEOUS COMPETITOR AND THE APPLICATION OF FERTILIZER IN
SOUTHEAST ALASKA

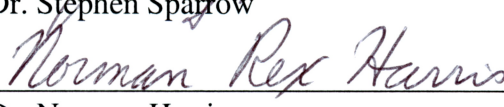
By

Emily Dickson

RECOMMENDED:



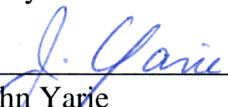
Dr. Stephen Sparrow



Dr. Norman Harris



Dr. Valerie Barber
Advisory Committee Chair

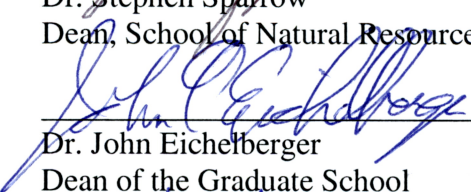


Dr. John Yarie
Chair, Department of Forest Sciences

APPROVED:



Dr. Stephen Sparrow
Dean, School of Natural Resources and Agricultural Sciences



Dr. John Eichelberger
Dean of the Graduate School



Date

GROWTH RESPONSE OF LUTZ SPRUCE SAPLINGS TO THE REMOVAL OF A
HERBACEOUS COMPETITOR AND THE APPLICATION OF FERTILIZER IN
SOUTHEAST ALASKA

A
THESIS

Presented to the Faculty
of the University of Alaska Fairbanks
in Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

By

Emily Dickson, B.S.

Fairbanks, Alaska

August 2014

Abstract

Herbaceous competitor species such as fireweed can impact future survival and growth of Lutz (*Picea x lutzii* Little, Pinaceae) spruce saplings. Fertilizer is applied to crop trees in order to supply more nutrients to promote growth. However, fertilizer benefits competitor species as well. Literature regarding the impacts of competition for resources between fireweed and spruce saplings are lacking, but the impacts of resource competition on seedling growth and fireweed are documented as significant. Seedlings are distinguished from saplings by differences in height and/or diameter. In order to test the influence of both competitor species and added fertilizer, we analyzed growth response of Lutz spruce saplings to fireweed removal and applied fertilizer through treatments and controls using a two by two factorial experiment. Results revealed that fireweed removal had a positive effect on sapling growth response, while added fertilizer alone showed no effect on sapling growth response. I found a strong, positive correlation between soil moisture and fireweed cover. I also found a strong, positive relationship between sapling growth and soil moisture as well as sapling growth and fireweed cover. This study demonstrates that spruce saplings positively responded to fireweed removal compared to the application of fertilizer. More importantly, the overall conclusion is that when saplings are not N limited soil, moisture is the driving factor in sapling height growth. The long-term effects of harvesting an efficient nitrogen competitor species are not well known and could be detrimental to future site fertility.

Table of Contents

	Page
Signature Page	i
Title Page	iii
Abstract	v
Table of Contents	vii
List of Figures	ix
List of Tables	xi
Acknowledgements	xiii
1.1 Introduction.....	1
1.2 Materials and Methods.....	6
1.2.1 Study Site	6
1.2.2 Experimental Procedure	7
1.2.3 Statistical Analyses	11
1.3 Results.....	13
1.3.1 Sapling Growth Response	13
1.3.2 Foliar and Soil Nitrogen.....	15
1.3.3 Fireweed Coverage.....	17
1.3.4 Soil Moisture and Temperature.....	20
1.4 Discussion	24
1.5 Conclusions.....	27
1.6 References.....	28

Lists of Figures

	Page
Figure 1: Normalized growth response of Lutz spruce saplings to treatments applied in 2006 in SE Alaska.....	15
Figure 2: Regression analysis between Lutz spruce sapling height and fireweed abundance from SE Alaska.....	18
Figure 3: Regression analysis between Lutz spruce normalized sapling growth response and fireweed abundance from SE Alaska.....	19
Figure 4: Correlation analyses between fireweed abundance and average soil moisture from SE Alaska	20
Figure 5: Regression analysis between Lutz spruce sapling height and average soil moisture content from SE Alaska	22
Figure 6: Regression analysis between Lutz spruce normalized sapling growth response and average soil moisture content from SE Alaska	23

Lists of Tables

	Page
Table 1: Agriform 20-10-5 Fertilizer Tablets Plus Minor Elements	8
Table 2: Fertilization rate of 20-10-5 Scott Agriform fertilizer pellets per sapling.....	8
Table 3: ANOVA summary of normalized Lutz spruce sapling growth response to treatments .	13
Table 4: Mean \pm S.D. of pre- and post-treatment growth rates and normalized growth response of Lutz spruce saplings for each treatment plot in SE Alaska	14
Table 5: Mean \pm S.D. of Lutz spruce needle and fireweed total nitrogen content of each treatment collected in August from 2006 through 2009 in SE Alaska	16
Table 6: Mean \pm S.D. of total soil nitrogen content from each treatment collected at the end of August from 2006 through 2008 in SE Alaska.....	17
Table 7: Mean \pm S.D. of average soil moisture and temperature for each treatment plot in SE Alaska	21

Acknowledgements

I would like to thank the land owner R. Schnabel for allowing me to conduct research on his land. A special thanks to V. Barber, S. Sparrow, N. Harris, and D. Valentine for their thoughtful comments and proofreading this manuscript. I'm also grateful for field assistance and support from J. Lieberman, E. Merklin, J. Potratz, L. Dwor, K. Zahnow, C. King, K. King, E. Karlsson-Ciosek, and many more. *This report is based upon work supported by the University of Alaska and Cooperative State Research, Education and Extension Service (now the National Institute of Food and Agriculture (NIFA)), U.S. Department of Agriculture, under Agreement No. 2005-34158-16547, 2006-34158-17722, 2008-34158-19474. Any opinions, findings, conclusions, or recommendations expressed in this publication are those of the author(s) and do not necessarily reflect the view of the U.S. Department of Agriculture.*

1.1 Introduction

Forest managers are faced with issues regarding herbaceous competitor species which can impact future survival and growth of planted seedlings during the establishment stage (Bell et al. 2000, Shropshire et al. 2001, Hangs et al. 2002, Matsushima and Chang 2006, Cortini and Comeau 2007, Man et al. 2008). Managers attempt to reduce competition from herbaceous species and stimulate seedling productivity through vegetation management practices, such as herbicides, disc-trenching, manual vegetation brushing (Boateng et al. 2006, Wagner and Robinson 2006, Cortini and Comeau 2007, Man et al. 2008) and application of nitrogen (N) fertilizer (Shropshire et al. 2001, Hangs et al. 2002, Hangs et al. 2003a, Staples et al. 1999, Haase et al. 2007). However, applied fertilizer can also benefit herbaceous competitors (Nams et al. 1993, Staples et al. 1999, Arie and Turkington 2002).

The application of fertilizer can cause a growth response in spruce and the effect has been reported as early as the first growing season after application. Van Cleve and Zasada (1976) reported a greater basal area of 70 year old white spruce after the first growing season of initial fertilizer treatment, while greater stem length and diameter were recorded in white spruce seedlings after two growing seasons in a greenhouse study (Phipps 1977). Other research suggests that the addition of N rich-fertilizer results in larger needles as well as greater needle N content and that it takes two to four years to see the growth response in fertilized pine trees ranging from 9 to 14 year old stand (Valentine and Allen, 1990).

Currently, no data exists on the competition between fireweed and spruce saplings for light, soil moisture, and resources or how fireweed impacts sapling growth. However, many studies (Bianco 1990, Hangs et al. 2002, Hangs et al. 2003b, and Staples et al. 1999) suggest there are significant impacts to seedling growth caused by competition from fireweed. The

difference between a seedling and a sapling has to do with height and/or diameter. Henceforth when referring to a seedling versus a sapling, the following is how they are defined. The seedling stage is when the cotyledon (first leaf or whorl of leaves developed by the embryo of a seed plant) has emerged from the seed and ends when the seedling reaches a height of 137 centimeters, known as diameter at breast height (dbh). Diameter at breast height is where a tree's diameter is measured. A sapling is taller than 137 centimeters (T. Malone, personal communication, 2014) and usually less than 2.54 cm in dbh (J.A. Yarie, personal communication, 2014) and is unable to reproduce (T. Malone, personal communication, 2014).

Planted conifer seedlings are small and experience low growth rates while herbaceous species can establish quickly, have high-growth and reproductive rates, and can be efficient competitors (Shropshire et al. 2001). Planted conifer seedlings are less effective at taking up N compared to herbaceous species (Arii and Turkington 2002, Hangs et al. 2003b, Hangs et al. 2004). This limitation can be of major consequence to conifers in northern forests because here N is considered to be the limiting factor controlling conifer seedling growth (Finlay et al. 1992, Hangs et al. 2004, Rygiewicz et al. 1984, Nams et al. 1993). The early stages of growth are crucial for crop seedlings because main stem growth is taking place, as in individual crown development such as crown depth and width. These traits are simple indicators that require minimal measurements from forest managers to determine future growth and development of individual crop trees (Sterck et al. 2003).

Crop tree species in northern Alaskan forests consist primarily of conifers including white spruce (*Picea glauca* (Moench) Voss Pinaceae), Sitka spruce (*P. sitchensis* (Bong.) Carr, Pinaceae), and Lutz spruce (*Picea x lutzii* Little, Pinaceae). Lutz spruce is a naturally occurring hybrid between Sitka and white spruce and grows in coastal, temperate forests in southeast

Alaska. Whole tree morphology of Lutz spruce is similar to white spruce, though cone size and cone-scale structure are more similar to Sitka spruce (Copes and Beckwith 1977). Sitka spruce trees have shallow roots with a long lateral spread and minor branching; roots may extend down two meters into the ground on deep, well-drained soils (Harris 1966 and 1990). In Northern forests, including Alaska white spruce roots are commonly within 15 centimeters of the organic-mineral soil interface (Nienstaedt and Zasada 1990). The root system of Lutz spruce is between Sitka and white spruce in depth. Therefore, it is reasonable to assume that during the sapling stage, before spruce roots have fully developed to that of a mature tree, they might overlap with roots of herbaceous species.

In Alaska, fireweed (*Chamerion angustifolium* (L.) Holub Onagraceae) is one of the most frequent herbaceous competitors to spruce saplings. Fireweed is a typical competitor-ruderal species (i.e., first to colonize disturbed sites such as recently burned or timber harvested sites). It is capable of rapid nutrient absorption and rapid root and growth rates (Chapin 1980). Fireweed has rhizome-like roots that can extend as deep as 45 centimeters, but most grow to a depth between 0 – 15 centimeters (Moss 1936, Hungerford 1986, Messier and Kimmins 1991). Fireweed reaches full height and maturity in one growing season and can colonize a site within two-five years, depending on site conditions. Lateral spread of fireweed roots is approximately one meter per year (Bianco 1990, Forest Practices Branch, Ministry of Forests, Province of British Columbia, 1997). Roots can occupy large areas of soil through extensive colonization and capitalize on available resources, achieving much greater growth and reproductive rates than planted spruce seedlings (Shropshire et al. 2001). Planted spruce seedlings are often covered by fireweed, which ranges up to three meters in height. Three years after colonization, fireweed reaches its maximum ground cover unless it is shaded out by tree and shrubs. If fireweed is not

shaded out it can persist for 10 to 30 years in an open canopy forest (Bianco 1990, Forest Practices Branch, Ministry of Forests, Province of British Columbia, 1997).

Fireweed has a competitive advantage over commercially valuable spruce seedlings and impacts their future survival and growth by reducing light, moisture availability, and soil resources (e.g. nitrogen and root space). Fireweed contributes to the bending and breaking of planted spruce seedlings when large, dense colonies of fireweed stems die and cover seedlings (Bianco 1990). For shade-tolerant species, including white spruce (Benzie and Blum 1989 and Day 1972), fireweed ground cover less than 50 percent is acceptable and diameter growth reduction and mortality is minimal (Bianco 1990). The maximum growth rate for shade-tolerant species is attainable at light levels as low as 40 percent of full sunlight (Lieffers and Stadt 1994).

In the presence of full sunlight, fireweed colonizes areas associated with a high soil moisture, (Bianco 1990, Forest Practices Branch, Ministry of Forests, Province of British Columbia, 1997), and high nitrate (NO_3^-) availability (Chapin 1980, Klinka et al. 1989), as fireweed is able to rapidly absorb nitrate (Staples et al. 1999, Hangs et al. 2002, Hangs et al. 2003b). Fireweed tends to out-compete planted white spruce seedlings for applied N fertilizer (Hangs et al. 2003b, Staples et al. 1999). Fireweed can absorb NO_3^- and ammonium (NH_4^+) simultaneously, compared to white spruce seedlings, which have a limited capacity for absorbing NO_3^- even after NH_4^+ is depleted. Moreover, fireweed generally has higher uptake rates for NH_4^+ and NO_3^- compared to white spruce, and thus has a competitive advantage in areas where N is the limiting factor of growth (Hangs et al. 2003b).

While the competitive advantage of fireweed over planted spruce seedlings is well known, there is little information available regarding the effects of competition on spruce saplings, the ecological impacts of harvesting fireweed from the site and how removal of

fireweed affects spruce sapling growth. Fireweed is one of many non-timber forest products (NTFPs) removed from forests annually, although fireweed is harvested in a limited capacity compared to other more economical products such as blueberries (*Vaccinium spp.*) or birch bark. Fireweed has many food and medicinal uses. In my study area, it was harvested to make herbal tea (Schofield 1993). Because repeated annual harvesting of fireweed can reduce competition for N, it is reasonable to assume this could result in enhanced spruce sapling productivity. On the other hand, it is possible that the removal of fireweed (during peak biomass production) could reduce future site productivity through the loss of available N instead of allowing the absorbed N to be cycled back through the forest system. Fireweed is a perennial plant, when only its leaves and petals are harvested regrowth is slowed, whereas when the entire aboveground portion of the plant (stem, leaves, and petals) is harvested its annual growth is halted for the rest of the growing season (Forest Practices Branch, Ministry of Forests, Province of British Columbia, 1997).

The overall objective of this study was to characterize the growth response of Lutz spruce saplings to fireweed removal and the application of fertilizer. The results of this study will assist timber managers in determining whether harvesting of fireweed, coupled with the application of fertilizer, is beneficial to planted crop trees' growth and survival. In this study, I compared the effects of fireweed removal and applied fertilizer separately and together, on sapling growth. I also examined the effect of fireweed removal and fertilizer application on the total N content of sapling needles, soil, and fireweed. Other objectives are to quantify the effects fireweed removal has on soil moisture and temperature, which can influence sapling growth.

I tested the hypothesis that Lutz spruce saplings will grow most quickly when herbaceous competitor species are removed coupled with the addition of fertilizer. More specifically, I hypothesize that the combined removal of fireweed and added fertilizer will result in an

increased total N content of needles, soil, and fireweed (non-removal plots) due to added fertilizer. Lastly, I hypothesize that fireweed removal will improve growing conditions by potentially reducing competition for resources such as soil moisture and nutrients.

1.2 Materials and Methods

1.2.1 Study Site

My research site was located approximately 42 kilometers north of Haines, Alaska, USA (59°24'N, 136°00'W) in a transition zone between a maritime and dry, cold continental climate. Average annual precipitation is approximately 1000 millimeters and average snowfall per season is around 3000 millimeters. The average temperature in January is -4 °C and 15 °C in July. Growing degree days exceed 1500 days (5 °C base temperature) (McCloskey 1998).

My study was conducted on a 16-hectare forest stand on flat terrain at an elevation of 85 meters, surrounded by mountains up to 2100 meters in altitude. The area was dominated by Sitka spruce, western hemlock (*Tsuga heterophylla* (Raf.) Sarg., Pinaceae), and black cottonwood (*Populus balsamifera* L. ssp. *trichocarpa* (Torr. & A. Gray ex Hook) Brayshaw, Salicaceae). The soil association was Kupreanof-Foad Complex (2-20 percent slopes, McCloskey 1998). The taxonomic class for both the Kupreanof and Foad series is loamy-skeletal, mixed, superactive Typic Humicryods (Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture).

The study site was privately owned and logged in 1995 and 1996. Soil and unused timber were bulldozed into piles and burned. In 1996, the land owner contracted to have the site replanted in a 2.4 by 2.4 meter spacing with Lutz spruce seedlings. Seeds were collected locally and were identified by the planting contractor as Lutz spruce. A second planting (approximately

four months after the initial planting) was necessary due to lack of seedling survivorship and root development in the prior planting. The second planting consisted of seedlings obtained from the Silvaseed Company (Roy, Washington), where plug seedlings at the nursery spent one year in containers followed by one year in the ground prior to planting.

1.2.2 Experimental Procedure

I established eight 20 by 20 meter plots in the summer of 2006 using a random complete block design. Four of the eight plots were established on the south section of the stand while the remaining four plots were established on the north section. Each block had all treatments plus a control. Within each block, plots were approximately 30 meters apart. Treatments consisted of fireweed removal (R), added fertilizer (F), fireweed removal and added fertilizer (R-F) and a control (NR-NF). The number of Lutz spruce saplings per treatment plots was as follows: $R_{1,2} = 29,43$; $F_{1,2} = 58,44$; $R-F_{1,2} = 53,23$; and $NR-NF_{1,2} = 33,38$.

I added two tablets (21 grams each) of 20-10-5 Scott Agriform pellets (The Scotts Company LLC., Marysville, OH.), a two-year slow-releasing fertilizer at the base of each sapling in fertilized plots, as requested by private landowner. Table 1 illustrates the Agriform NPK fertilizer compounds plus minor nutrients applied once in May 2006. The fertilization rate for NPK fertilizer pellets is displayed in Table 2 on a per sapling basis.

Table 1. Agriform 20-10-5 Fertilizer Tablets Plus Minor Elements

Total nitrogen (N).....	20.0%
Urea nitrogen.....	2.40%
Water soluble organic nitrogen*.....	4.00%
Water insoluble nitrogen.....	13.6%
Citrate extractable phosphate (expressed as P ₂ O ₅)...	10.0%
Soluble potash (expressed as K ₂ O).....	5.00%
Calcium (Ca).....	3.30%
Magnesium (Mg) (Total).....	0.70%
Sulfur (S) (Total).....	2.00%
Combined sulfur (S).....	2.00%
Boron (B).....	0.04%
Copper (Cu) (Total)	0.05%
Water soluble copper (Cu).....	0.05%
Iron (Fe).....	0.90%
Water soluble iron (Fe).....	0.90%
Manganese (Mn) (Total).....	0.07%
Water soluble manganese (Mn).....	0.07%
Zinc (Zn) (Total).....	0.05%
Water soluble zinc (Zn).....	0.05%

Derived from: urea, methylene ureas, calcium phosphate, potassium sulfate, calcium sulfate, magnesium oxide, sodium borate, copper sulfate, iron sulfate, manganese sulfate, and zinc sulfate. *Contains 3.2% slowly available methylenediurea and dimethylenetriurea nitrogen.

Table 2. Fertilization rate of 20-10-5 Scott Agriform fertilizer pellets per sapling.

Treatment	Number of saplings	N per sapling (g)	P per sapling (g)	K per sapling (g)
NR-F	58,44	8.4	1.85	1.74
R-F	53,23	8.4	1.85	1.74

NR = no fireweed removal, R = fireweed removal, and F = fertilizer N = nitrogen, P = phosphorus, K = potassium, Number of saplings are illustrated as treatment replicate one and treatment replicate two.

Before harvesting fireweed, I measured the aerial cover (percent cover) of fireweed on all eight plots (2008 only) using a point-intercept method as described by Elzinga et al. (1998). I recorded the presence or absence of fireweed at approximately 120 grid points, spaced 1.5 meters apart for each plot. I harvested the entire above-ground portion of fireweed from all removal plots (20 by 20 meter plots) during peak biomass in late July to early August each year from 2006-2008. For nutrient analysis, fireweed samples were collected from all fireweed removal plots in 2006 and 2007 and from all treatment plots in 2008 and 2009. In 2009, I collected fireweed subsamples using the point-intercept method as previously described to determine if fireweed nutrient content changed over time from fireweed removal and/or added fertilizer treatments. To obtain data on nutrient content, leaves were stripped from the stem and dried to a constant mass. The only other disturbance was human foot traffic.

I measured annual internode growth and sapling height at the end of August each year to determine the growth response of spruce saplings to treatments. Annual internode growth from the previous 10 to 13 years was determined prior to treatments by measuring the distance between whorls. A small but consistent error in yearly growth response was introduced because of the way the internode distances were measured as previously described instead of the distance between the bottom of one year's whorl to the bottom of the prior year's whorl. I measured annual internode growth in 2006, 2007 and 2008. Sapling height was measured for all saplings at the end of 2006, 2007, and 2008 growing seasons. I used annual internode growth and tree height to determine pre- and post-treatment growth rates (cm/yr) and subsequently normalized growth response. I defined pre-treatment growth rates as $R_{pre} = 2005 \text{ sapling height} / \text{age of the sapling}$ and post-treatment growth rates as $R_{post} = \text{average internode growth per each year (2006, 2007, and 2008)}$. I determined the normalized sapling height growth response (also referred to as

sapling growth or sapling growth response) as $(R_{\text{post}} - R_{\text{pre}}) / (R_{\text{pre}})$ and then calculated the average on a whole-plot level. Sapling growth rates and growth response were then averaged on a per treatment plot basis to determine treatment means.

I installed two soil moisture smart sensors (S-SMA-M003, 2002-2011[®] Onset Computer Corporation, Cape Cod, Massachusetts, USA) and two 12-bit temperature smart sensors (S-TMB-M003, 2002-2011[®] Onset Computer Corporation, Cape Cod, Massachusetts, USA) for measuring volumetric (m^3/m^3) water content and soil temperature ($^{\circ}\text{C}$) in each plot, with one of each sensor located approximately two meters and ten meters from the center point of the plot. Measurements were taken five centimeters below the organic/mineral interface in each plot. Soil moisture and temperature were recorded once every three hours by a HOBO[®] Weather Station logger (2002-2011[®] Onset Computer Corporation, Cape Cod, Massachusetts, USA) from 2006 to 2009. Soil moisture and temperature data were calculated as an overall average (from 2006 to 2009) for each treatment plot from measurements collected at two meters and ten meters from the center plot, five centimeters below the organic/mineral soil interface.

I collected needles at the end of August from fertilized plots during the 2006 season (post-fertilization) from all plots during the 2007 and 2008 growing season for nutrient analysis. Samples were collected from the upper one-third of the south side of the crown from five randomly selected saplings per plot. All needles (~100 – 200 needles) from the selected branch were collected from the most recent growing season.

I analyzed soil samples for total N to quantify the effects of treatments. Four soil samples were collected from two depths from the surface, 0-5 centimeters and 5-10 centimeters, in all eight plots during 2006, 2007, and 2008. The soil collection points were ten meters NW, NE, SE, and SW from the center point of the plot. Samples were combined by depth (0-5 centimeters or

5-10 centimeters) and by treatment. They were dried to a constant mass at 65 ° C to obtain nutrient content. I analyzed needle, fireweed, and soil samples for total N on a LECO[®] CHN-1000 Analyzer (LECO Corporation, Michigan) and/or on a LECO[®] CNS-2000 Analyzer (LECO Corporation, Michigan) at the University of Alaska Fairbanks (UAF).

1.2.3 Statistical Analyses

To evaluate normalized sapling growth response (sapling height growth or growth response) to fireweed removal, added fertilizer, and fireweed removal x fertilizer treatments, I conducted an ANOVA ($N = 8$, SAS v9.2 SAS institute, Cary, North Carolina, 2009) analysis of all treatments against the control. All ANOVA analyses were run using a random complete block (RCB) design consisting of two block locations within the research area. ANOVA results are reported with the F value followed by the degrees of freedom of the numerator and the denominator as well as the P value. Regressions are reported with R^2 and P values while correlations are reported with r and P values. Unless otherwise specified all analyses were conducted using means on a whole-plot level. Because of our small sample size ($N= 8$) and low estimation power, we chose an alpha (α) of 0.1.

Fireweed removal and added fertilizer treatments could cause fluctuations in total needle, soil, and fireweed N (hence forth referred to as total foliar and soil N) content over time. I used separate ANOVA analyses on total foliar and soil N to determine the effects of treatments (fireweed removal, added fertilizer, and fireweed removal x added fertilizer) and year (2006, 2007, 2008, and 2009 (fireweed only) on total foliar and soil N. ANOVA analyses from total needle and fireweed N were completed with unequal sample sizes because no needle N data was collected from unfertilized plots during 2006 growing season (collections were from fertilized

plots only) and no fireweed N data was collected from non-fireweed removal plots during the 2006 and 2007 growing season (collections were from fireweed removal plots only).

Since fireweed density has been linked to a decrease in spruce growth (Bianco 1990), I used a regression analysis to determine the effects of fireweed cover on sapling height and fireweed cover on sapling height growth response. I explored this relationship further by evaluating the effects of treatments on fireweed cover using an ANOVA analysis. To further explore the impacts from fireweed coverage, I conducted a correlation analysis between fireweed coverage and average soil moisture as well as fireweed coverage and average soil temperature.

Fireweed tends to densely colonize moist, recently clear-cut or open forest stands (Bianco 1990, Forest Practices Branch, Ministry of Forests, Province of British Columbia, 1997); thus high densities of fireweed can indicate a moist site and low densities of fireweed may indicate a dry site (Forest Practices Branch, Ministry of Forests, Province of British Columbia, 1997). I assessed this relationship through separate ANOVAs, testing the effects of treatments on average soil moisture and temperature. I also assessed the relationship between average soil moisture and temperature on sapling height as well as average soil moisture and temperature on sapling height growth response using separate regressions.

1.3 Results

1.3.1 Sapling Growth Response

Sapling height growth was positively affected by fireweed removal ($F_{1,3} = 26.2, p = 0.01$) and the combined fireweed removal and added fertilizer ($F_{1,3} = 15.71, p = 0.03$). Fertilizer ($F_{1,3} = 1.3, p = 0.33$) alone showed no significant effect on spruce sapling growth response (Table 3). More specifically, sapling growth response was greater in plots where fireweed was removed relative to the control (Table 4 & Figure 1).

Table 3. ANOVA summary of normalized Lutz spruce sapling growth response to treatments.

Source of Variation	df	SS	MS	F	P
Block	1	0.0002	0.0002	0.11	0.76
Removal	1	0.0480	0.0481	26.2	0.01
Fertilizer	1	0.0024	0.0024	1.34	0.33
Removal*fertilizer	1	0.0288	0.0288	15.7	0.03
Error	3	0.0055	0.0018		
Total	7	0.0850			

ANOVA results show a fireweed removal effect ($p = 0.01$) to sapling growth but not a fertilizer effect ($p = 0.33$).

Table 4. Mean \pm S.D. of pre- and post-treatment growth rates and normalized growth response of Lutz spruce saplings for each treatment plot in SE Alaska.

Treatment	Mean (n = 2) Pre-Treatment Growth Rate (cm/yr) \pm S.D.	Mean (n = 2) Post-Treatment Growth Rate (cm/yr) \pm S.D.	Mean (n = 2) Normalized Sapling Growth Response \pm S.D.
NR-NF	17.3 \pm 2.90	30.8 \pm 5.15	0.83 \pm 0.04
R-NF	19.3 \pm 1.96	36.3 \pm 1.50	0.87 \pm 0.06
NR-F	18.7 \pm 0.74	30.9 \pm 0.66	0.68 \pm 0.03
R-F	14.7 \pm 0.21	28.6 \pm 0.03	0.95 \pm 0.02

NR = no fireweed removal, R = fireweed removal, NF = no fertilizer, and F = fertilizer. Data are means \pm SE. Pre-treatment growth rates are R_{pre} = 2005 sapling height / age of the sapling. Post-treatment growth rates are R_{post} = average node growth from 2006, 2007, and 2008. Normalized sapling growth response (also referred to as sapling height growth or sapling growth response) was defined as R_{post} (post-treatment growth rates – R_{pre} (pre-treatment growth rates) / R_{pre} (pre-treatment growth rates). Sapling height was measured for all saplings in 2006, 2007, and 2008 at the end of August. ANOVA results show a fireweed removal effect ($p = 0.01$) to sapling growth but not a fertilizer effect ($p = 0.33$).

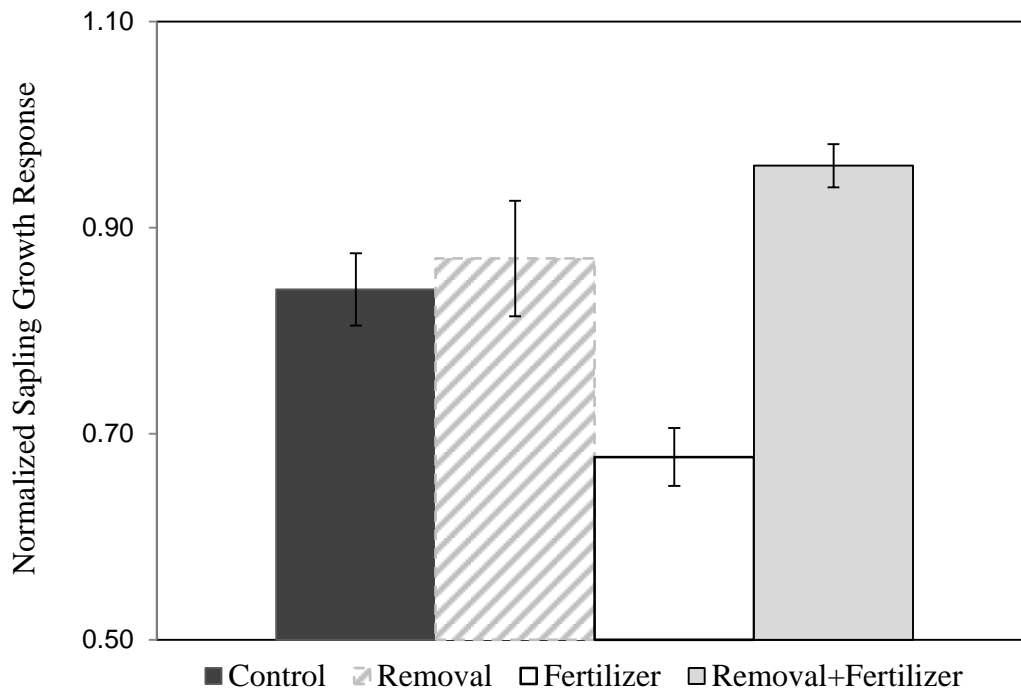


Figure 1. Normalized growth response of Lutz spruce saplings to treatments applied in 2006 in SE Alaska. Data are means \pm SE. Normalized sapling growth response (also referred to as sapling height growth or sapling growth response) was defined as R_{post} (post-treatment growth rates – R_{pre} (pre-treatment growth rates) / R_{pre} (pre-treatment growth rates). ANOVA results show a fireweed removal effect ($p = 0.01$) to sapling growth but not a fertilizer effect ($p = 0.33$).

1.3.2 Foliar and Soil Nitrogen

There were no significant treatment effects on total needle, soil, or fireweed N content (g/kg). Within a given year, no significant differences in spruce needle, fireweed, or soil (total) N content were detected (Table 5 & Table 6). There were no overall trends shown in foliar or soil (total) N among treatments over time.

Table 5. Mean \pm S.D. of Lutz spruce needle and fireweed total nitrogen content of each treatment collected in August from 2006 through 2009 in SE Alaska.

Total Needle N (g/kg)				
Year	2006	2007	2008	2009
NR-NF	--	11.4 \pm 1.49	9.40 \pm 1.13	--
R-NF	--	13.1 \pm 0.78	11.2 \pm 1.30	--
NR-F	10.2 \pm 0.56	11.5 \pm 0.35	9.60 \pm 1.20	--
R-F	10.4 \pm 0.30	12.3 \pm 0.35	10.1 \pm 0.71	--
Total Fireweed N (g/kg)				
Year	2006	2007	2008	2009
NR-NF	--	--	24.6 \pm 2.26	22.8 \pm 1.21
R-NF	24.6 \pm 3.5	20.7 \pm 2.48	20.7 \pm 1.84	20.3 \pm 0.85
NR-F	--	--	20.6 \pm 5.45	21.9 \pm 1.20
R-F	27.5 \pm 4.2	21.2 \pm 4.60	20.9 \pm 4.53	22.3 \pm 3.61

NR = no fireweed removal, R = fireweed removal, NF = no fertilizer, and F = fertilizer. Total needle nitrogen was determined from samples collected from 5 randomly selected Lutz spruce saplings from each treatment plot. Total fireweed nitrogen was determined from samples collected from each treatment plot. No significant differences in total foliar N among treatments within a given year ($\alpha = 0.1$).

Table 6. Mean \pm S.D. of total soil nitrogen content from each treatment collected at the end of August from 2006 through 2008 in SE Alaska.

Total Soil N (g/kg)						
Year	2006		2007		2008	
Depth	0-5 cm	5-10 cm	0-5 cm	5-10 cm	0-5 cm	5-10 cm
NR-NF	4.0 \pm 0.14	1.7 \pm 0.28	3.1 \pm 0.28	2.2 \pm 0.85	5.9 \pm 2.47	4.9 \pm 2.19
R-NF	4.1 \pm 1.34	1.1 \pm 0.34	5.4 \pm 1.20	4.9 \pm 1.06	5.5 \pm 0.42	4.7 \pm 1.41
NR-F	5.6 \pm 0.49	1.5 \pm 0.14	4.1 \pm 0.07	3.4 \pm 1.20	5. \pm 1.91	4.7 \pm 2.82
R-F	3.1 \pm 0.99	1.2 \pm 0.21	3.4 \pm 0.92	2.0 \pm 0.21	5.7 \pm 2.54	4.4 \pm 2.90

NR = no fireweed removal, R = fireweed removal, NF = no fertilizer, and F = fertilizer. Soil nitrogen content was determined from samples collected from both 0 -5 cm and 5 -10 cm in each treatment plot. No significant differences in total soil N among treatments within a given year ($\alpha = 0.1$).

1.3.3 Fireweed Coverage

Mean fireweed percent cover (\pm SD) for the control was 44.7 ± 15.2 , for fertilizer 47.7 ± 5.3 , for fireweed removal 42.7 ± 1.6 , and 33.3 ± 19.0 for the combined treatments. There were no significant treatment effects on fireweed cover. There was a significant, positive relationship between fireweed cover and sapling height (Figure 2, $R^2 = 0.40$, $p = 0.09$). There appears to be no relationship between normalized sapling growth response and fireweed cover (Figure 3, $R^2 = 0.89$, $p = 0.23$). However, I found a positive correlation between fireweed cover and soil moisture (Figure 4, $r = 0.79$, $p = 0.02$).

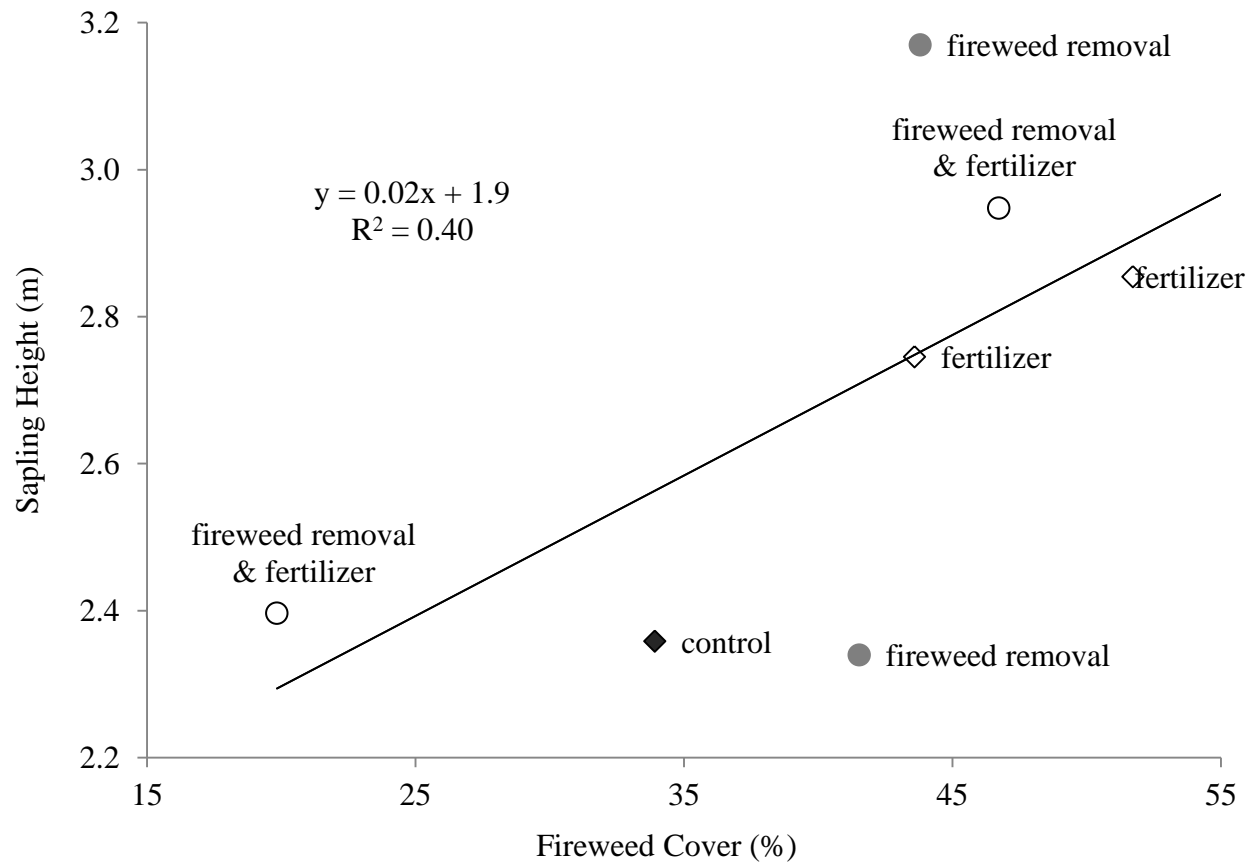


Figure 2. Regression analysis between Lutz spruce sapling height and fireweed abundance from SE Alaska. Fireweed abundance data are displayed as an average collected using grid points from per plot in 2008. Sapling height was measured for all saplings in the 2006, 2007, and 2008 at the end of August. Sapling height displayed in this data set is the mean per treatment from the 2008 growing season. $p = 0.09$.

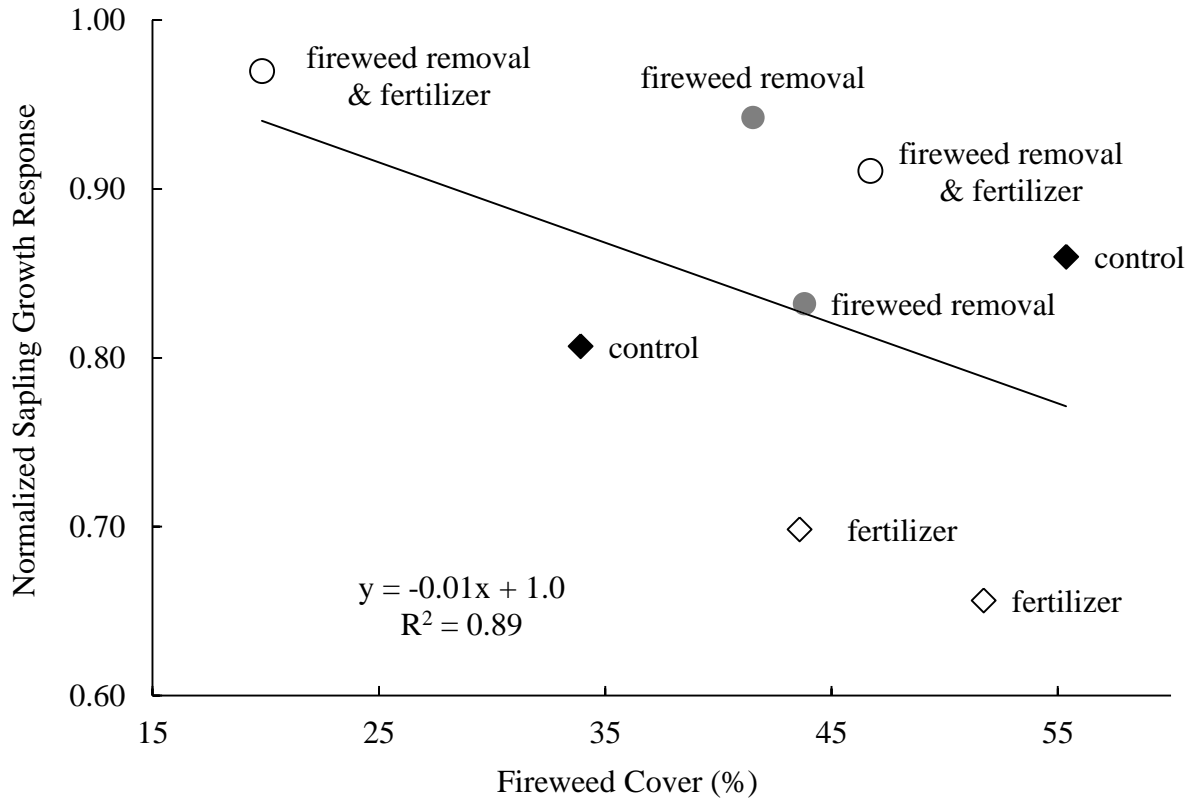


Figure 3. Regression analysis between Lutz spruce normalized sapling growth response and fireweed abundance from SE Alaska. Normalized sapling growth response (also referred to as sapling height growth or sapling growth response) was defined as R_{post} (post-treatment growth rates – R_{pre} (pre-treatment growth rates) / R_{pre} (pre-treatment growth rates). Fireweed abundance data are displayed as an average collected using grid points from per plot in 2008. $p = 0.23$.

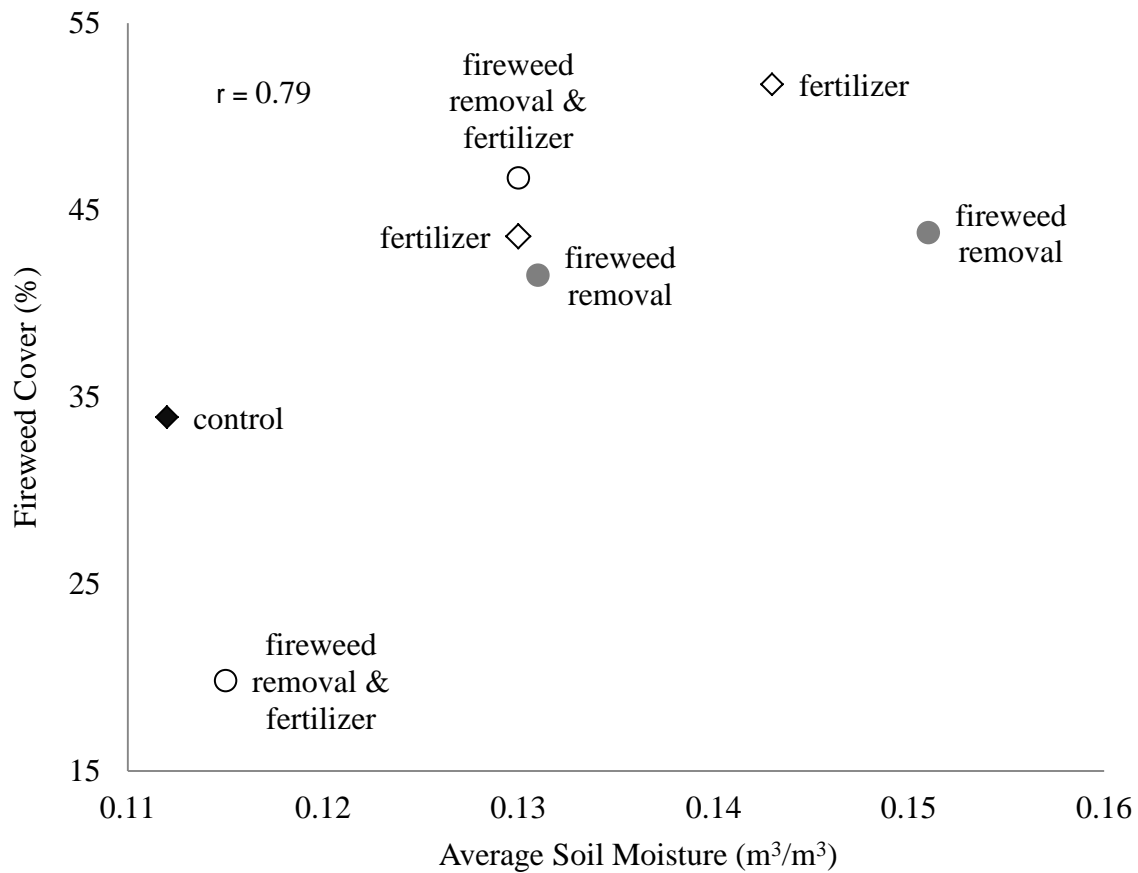


Figure 4. Correlation analyses between fireweed abundance and average soil moisture from SE Alaska. Fireweed coverage data are displayed as an average collected using grid points from per plot from 2008. Soil moisture data was collected at 2 m and 10 m from the center plot, 5 cm below the organic and mineral soil interface at every three hours from 2006 through 2009 and displayed as an overall average. $p = 0.02$

1.3.4 Soil Moisture and Temperature

Treatments showed no difference in average soil moisture among fireweed removal ($F_{1,3} = 0.01$, $p = 0.92$), added fertilizer ($F_{1,3} = 0.30$, $p = 0.62$) and fireweed removal x added fertilizer ($F_{1,3} = 1.48$, $p = 0.31$) treatments. A strong trend of increased sapling height with increased soil moisture (Table 6, Figure 5, $R^2 = 0.83$, $p = 0.002$) was detected. There was no significant relationship between normalized sapling growth response and average soil moisture (Figure 6, R^2

= 0.04, $p = 0.63$). No significant differences in average soil temperature among treatments: fireweed removal ($F_{1,3} = 1.08$, $p = 0.37$), added fertilizer ($F_{1,3} = 0.74$, $p = 0.45$) and fireweed removal x added fertilizer ($F_{1,3} = 0.02$, $p = 0.91$) were detected. I found no relationship between sapling height and soil temperature ($R^2 = 0.31$, $p = 0.15$) or between sapling growth response and soil temperature ($R^2 = 0.05$, $p = 0.31$).

Table 7. Mean \pm S.D. of average soil moisture and temperature for each treatment plot in SE Alaska.

Treatment	Average Soil moisture (m ³ /m ³)	Average Soil temperature (°C)
NR-F	0.137 \pm 0.01	5.47 \pm 0.64
R-F	0.123 \pm 0.01	4.67 \pm 0.96
R-NF	0.141 \pm 0.01	5.28 \pm 0.71
NR-NF	0.130 \pm 0.02	6.22 \pm 3.96

NR = no fireweed removal, R = fireweed removal, NF = no fertilizer, and F = fertilizer. Soil moisture and temperature data was collected at 2 m and 10 m from the center plot, 5 cm below the organic and mineral soil interface. Data was collected every three hours from 2006 through 2009 and displayed as an overall average. No significant differences in soil moisture or temperature among treatments ($\alpha = 0.1$).

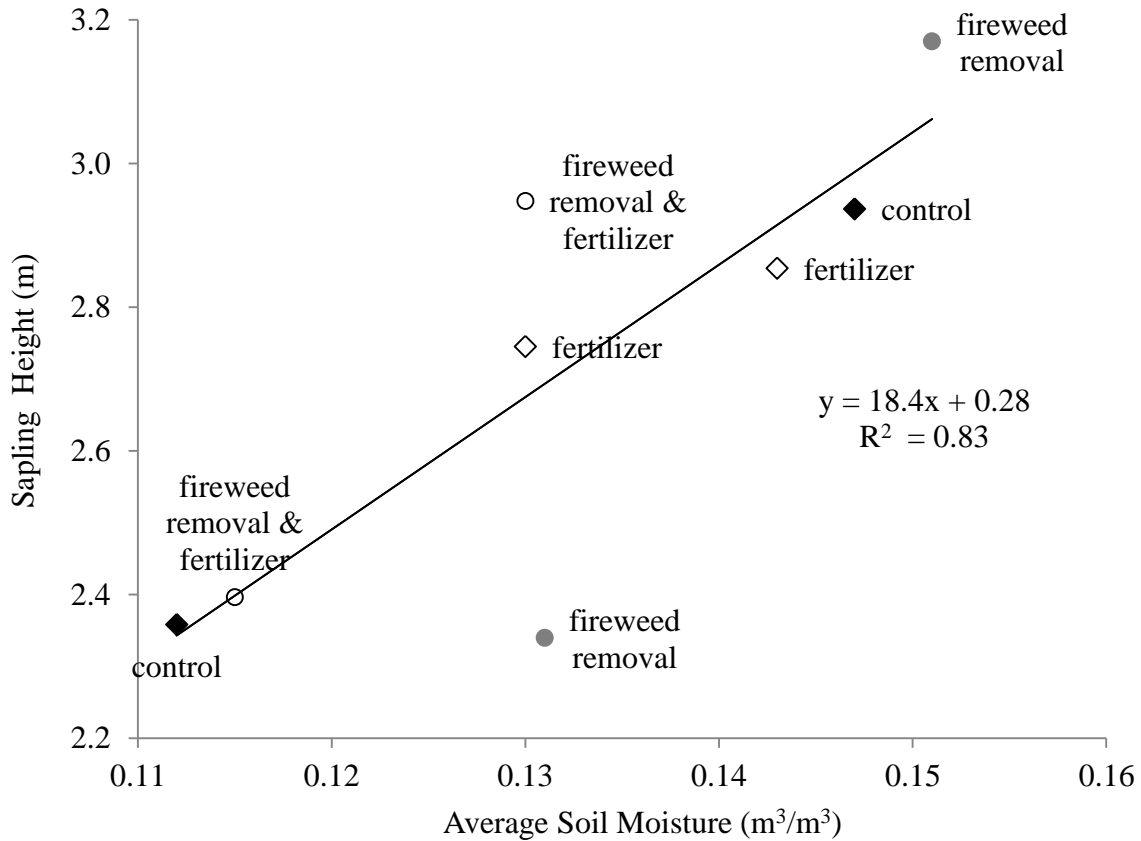


Figure 5. Regression analysis between Lutz spruce sapling height and average soil moisture content from SE Alaska. Sapling height was measured for all saplings in the 2006, 2007, and 2008 at the end of August. Sapling height displayed in this data set is the mean per treatment from the 2008 growing season. Soil moisture data is displayed as means per treatments and collected at both 2 m and 10 m from the center plot, 5 cm below the organic and mineral soil interface at every three hours from 2006 through 2009 and displayed as an overall average. $p = 0.01$.

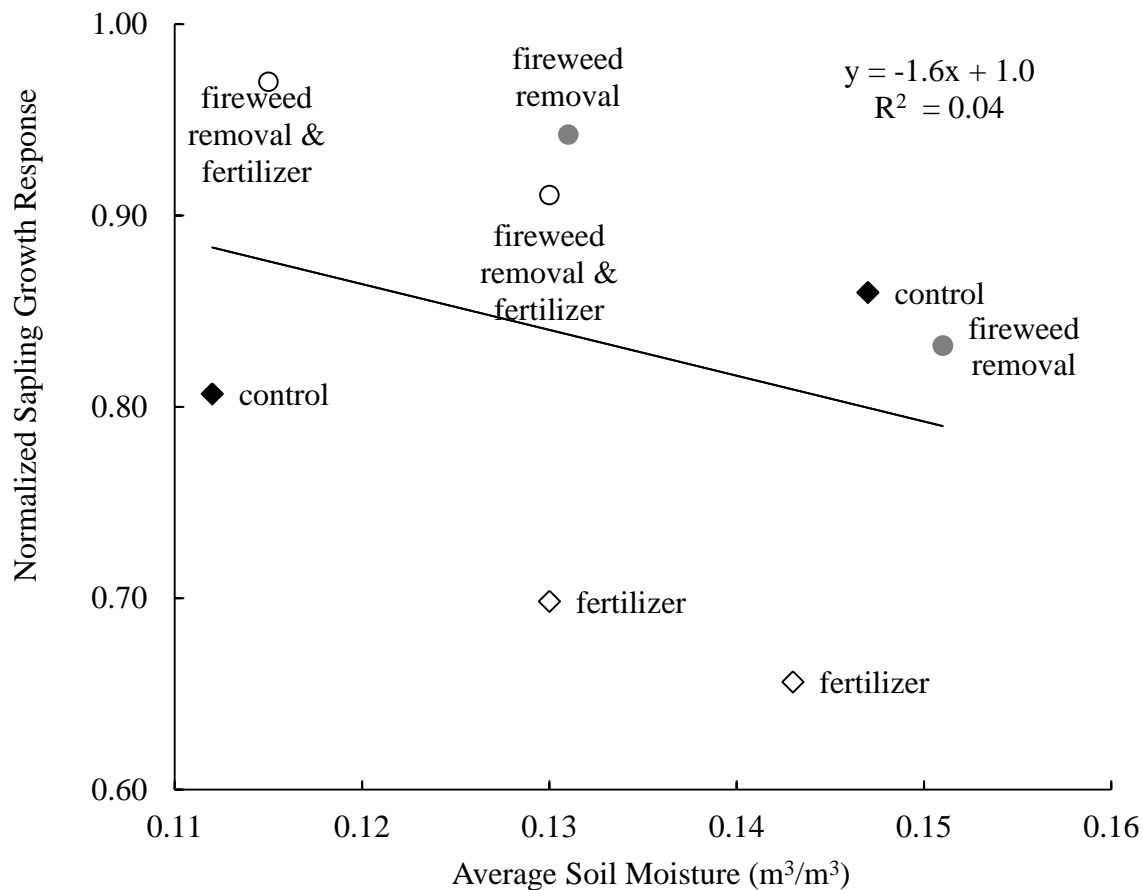


Figure 6. Regression analysis between Lutz spruce normalized sapling growth response and average soil moisture content from SE Alaska. Normalized sapling growth response (also referred to as sapling growth response) was defined as R_{post} (post-treatment growth rates – R_{pre} (pre-treatment growth rates) / R_{pre} (pre-treatment growth rates). Soil moisture data is displayed as means per treatments and collected at both 2 m and 10 m from the center plot, 5 cm below the organic and mineral soil interface at every three hours from 2006 through 2009 and displayed as an overall average. $p = 0.63$.

1.4 Discussion

Saplings growing in fireweed removal plots experienced greater growth relative to saplings growing in the control, while I was unable to detect a significant growth response to fertilizer alone. These results might indicate that there may be a degree of competition for resources between spruce saplings and fireweed. The removal of fireweed can reduce competition for resources, although it is unknown if the degree of competition observed in my study was less than that experienced in the seedling stage (prior to the start of study), which is when other researchers conclude that competition for N with herbaceous species is more likely to occur (Bianco 1990, Hangs et al. 2002, Hangs et al. 2003b, and Staples et al. 1999). The positive growth response in spruce saplings is likely attributable to the reduction of competition between fireweed and spruce saplings for resources due to the removal of fireweed.

Reducing competition for nutrient resources through fireweed removal and/or added fertilizer should result in higher needle N content and, indirectly, through a higher sapling growth rate. I would expect to see higher N content in spruce needles with fireweed removal and especially with added fertilizer when N is limiting on the site. However, my results indicate that this research site was probably not N limited. This could be why I did not detect a higher N content in spruce saplings due to fertilizer treatments. If my site is not N deficient, it would make little difference if the amount of fertilizer added was low ($0.10\text{--}1.2\text{ g/m}^2$ per plot) such as in this study or if the fertilization rate was higher as in other studies ($38\text{--}47\text{ g/m}^2$ or $45\text{--}136\text{ kg/ha}$ of N) where growth response to fertilizer was significant (Van Cleve and Zasada 1976, and Phipps 1977).

Adequate N could also explain why I did not detect any significant differences in fireweed and soil N between treatments within a given year. It is important to note that sampling

locations were different than where the fertilizer was placed. Fertilizer was applied at the base of each sapling while soil and fireweed N samples were collected at random points in the plot and not at the base of each sapling where differences were more likely to be detected. Even if samples were collected near fertilized points it is possible that I still would not detect an increase in total N due to added fertilizer because site contained adequate N. Additionally, my needle N content data also indicates that my site is not N deficient but may, in fact, be fertile. My results indicated that needle N content in spruce was within range of the N level of 10 g/kg, where it is considered to be a typical level in Interior Alaska (J.A. Yarie, personal communication, 2009).

Fireweed tends to grow on forest stands associated with moderate to high fertility (Chapin 1980, Bianco 1990, Staples et al. 1990, Hangs et al. 2002, Hangs et al. 2003b) and an abundance of soil moisture (Bianco 1990, Forest Practices Branch, Ministry of Forests, Province of British Columbia, 1997) thus plots with higher rates of fireweed cover are likely to be more fertile with higher soil moisture, thereby supporting greater sapling growth. My results are consistent with this observation that these sites are moisture limited and not nutrient limited. Regardless of fireweed removal or N additions, plots with greater soil moisture supported higher rates of fireweed cover and produced taller spruce saplings. Furthermore, my results indicate that soil moisture content is the driving factor for sapling growth when nutrients are not limited. This positive relationship between fireweed cover and soil moisture is supported by previous research from Bianco 1990 and the Forest Practices Branch, Ministry of Forests, Province of British Columbia, 1997, where they found that areas with abundant soil moisture and nutrients were considered to be problem sites for conifers because of high competition with fireweed. This coincides with my earlier statement that a high cover of fireweed could be linked to site fertility (conditions that favor tree and vegetation growth).

Sapling growth response did not show a relationship with fireweed cover or with soil moisture. This could be due to temporal and spatial inconsistencies in my measurements, which could have failed to show changes due to treatments. As mentioned in my methods section, fireweed cover was only measured once during treatments (the 3rd year after initial treatments) while, soil moisture measurements were averaged over the growing season instead of pre- and post-fireweed removal. If pre- and post- soil moisture and fireweed data were obtained it could have better illustrated the dynamics between fireweed removal and soil moisture and the impacts of sapling growth response to treatments. However, my data showed no relationship between sapling growth response and fireweed cover or between sapling growth response and soil moisture.

It is also important to consider the response of spruce saplings to fluctuations in resources. Stress-tolerant species like spruce have adapted to withstand competitor species and are less likely to respond to temporary fluctuations in nutrients. Spruce trees have adopted a “nutrient-stress tolerant strategy”, including slow nutrient absorption, slow root growth, and small nutrient loss compared to the competitive-ruderal strategy of fireweed where there is rapid nutrient absorption, rapid root growth, and large nutrient loss. Spruce that experience a recent flush of nutrients tend to maintain nutrient reserves instead of exhibiting a large growth response, which allows for sapling survival during periods of low nutrient availability (Chapin 1980).

1.5 Conclusions

Interpretations from this study are statistically limited due to small sample size ($N = 8$ plots) and little replication (two replicates per treatment), which gave low statistical power to detect differences among treatments. A future study design should include sufficient replication of each treatment and better linkage of spatial and temporal measurements. My results do demonstrate that spruce saplings benefited from fireweed removal and apparently not from added fertilizer. If spruce saplings were not N limited the addition of fertilizer would do little to benefit sapling growth but could further stimulate the growth of fireweed. My results showed that soil moisture was a major driving factor for sapling height growth on the study site. Results from this study indicate that the removal of herbaceous competitor species is more beneficial for increasing spruce yields compared to the addition of fertilizer. Although no cost-benefit analysis literature exists, it is unlikely that the removal of fireweed is an economically feasible choice to promote the growth of crop trees unless the fireweed is being used for other economic gains in value-added products. Furthermore, forest managers growing Lutz spruce saplings on shallow soils need to test for nitrogen before applying fertilizer. If nitrogen is limiting, they should reconsider the application of N-rich fertilizers unless herbaceous competitor species are removed beforehand because the fertilizer is more likely to benefit fireweed than conifers (Staples et al. 1999, Hangs et al. 2002, Hangs et al. 2003b). Lastly, more research is needed to address the long-term effects of the removal of herbaceous competitor species and its effect on long-term site fertility, which was beyond the scope of this study.

1.6 References

- Arii, K., and R. Turkington. 2002. Do nutrient availability and competition limit plant growth of herbaceous species in the boreal forest species understory ? Arctic, Antarctic and Alpine Research. 34(3): 251–261. doi:0.2307/1552482.
- Bell, F.W., M.T. Ter-Mikaelian, and R.G. Wagner. 2000. Relative competitiveness of nine early-successional boreal forest species associated with planted jack pine and black spruce seedlings. Can. J. For. Res. 30(5): 790–800. doi: 10.1139/cjfr-30-5-790.
- Benzie, J.W., and B.M. Blum. 1989. Silviculture of northeastern conifers. In: Burns, Russell M., compiler. The scientific basis for silvicultural and management decisions in the National Forest System. Gen. Tech. Rep. WO-55. Washington, DC: U.S. Department of Agriculture, Forest Service: 18-30. Available from <http://www.fs.fed.us/database/feis/plants/tree/larlar/all.html>[accessed 18 June 2014].
- Bianco, J. 1990. Managing fireweed on problem coastal sites. Laing & McCulloch, Forest Management Services, Smithers B.C. FRDA 163.
- Boateng, J.O., J.L. Heineman, J. McClarnon, and L. Bedford. 2006. Twenty year responses of white spruce to mechanical site preparation and early chemical release in the boreal region of northeastern British Columbia. Can. J. For. Res. 36: 2386–2399. doi:10.1139/X06-197.
- Chapin, S.F. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics. 11: 233–260. doi:10.1146/annurev.es.11.110180.001313.
- Copes, D.L., and R.C. Beckwith. 1977. Isoenzyme identification of *Picea glauca*, *P. sitchensis*, and *P. lutzii* populations. Bot. Gaz. 138(4): 512-521. Available from <http://www.jstor.org/stable/2473888>[accessed 23 April 2014].
- Cortini, F., and P.G. Comeau. 2007. Evaluation of competitive effects of green alder, willow and other tall shrubs on white spruce and lodgepole pine in Northern Alberta. For. Ecol. Manage. 255(1): 82–91. doi:10.1016/j.foreco.2007.08.027.
- Day, R.J. 1972. Stand structure, succession, and use of southern Alberta's Rocky Mountain forest. Ecology. 53(3): 472-478. doi:10.2307/1934235.

Elzinga, C.L., D.W. Salzer, and J.W. Willoughby. 1998. Measuring & Monitoring Plant Populations. U.S. Department of the Interior, Bureau of Land Management. BLM Technical Reference 1730-1. BLM/RS/ST-98/005+1730.

Finlay, R.D., A. Frostegard, and A.M. Sonnerfeldt. 1992. Utilization of organic and inorganic nitrogen sources by ectomycorrhizal fungi in pure culture and in symbiosis with *Pinus contorta* Dougl. ex Loud. *New Phytol.* 120(1): 105–115. doi:10.1111/j.1469-8137.1992.tb01063.x.

Forest Practices Branch, Ministry of Forests, Province of British Columbia. 1997. Operational summary for fireweed complex. Available from <http://www.for.gov.bc.ca/hfp/publications/00047/fireweed.pdf> [accessed 9 May 2013].

Haase, D.L., P. Alzugaray, R. Rose, and D.F. Jacobs. 2007. Nutrient-release rates of controlled-released fertilizer in forest soil. *Commun. Soil Sci. and Plant Anal.* 38(5-6): 739–750. doi:10.1080/00103620701220692.

Hangs, R.D., J.D. Knight, and K.C.J. Van Rees. 2002. Interspecific competition for nitrogen between early successional species and planted white spruce and jack pine seedlings. *Can. J. For. Res.* 32(10): 1813–1824. doi:10.1139/X02-100.

Hangs, R.D., J.D. Knight, and K.C.J. Van Rees. 2003a. Nitrogen accumulation by conifer seedlings and competitor species from ¹⁵nitrogen-labeled controlled-release fertilizer. *Soil Sci. Soc. Am. J.* 67(1): 300–308. doi:10.2136/sssaj2003.3000.

Hangs, R.D., J.D. Knight, and K.C.J. Van Rees. 2003b. Nitrogen uptake characteristics for roots of conifer seedlings and common boreal forest competitor species. *Can. J. For. Res.* 33(1): 156–163. doi:10.1139/X02-169.

Hangs, R.D., K.J. Greer, and C.A. Sulewski. 2004. The effect of interspecific competition on conifer seedling growth and nitrogen availability measured using ion-exchange membranes. *Can. J. For. Res.* 34(3): 754–761. doi:10.1139/X03-229.

Harris, A.S. 1966. Effects of slash burning on conifer regeneration in southeast Alaska. Research Note NOR-18. Juneau, AK: U.S. Department of Agriculture, Forest Service, Northern Forest Experiment Station. pp. 6.

Harris, A.S. 1990. *Picea sitchensis* (Bong.) Carr. Sitka spruce. In Burns, Russell M., and Barbara H. Honkala, tech. coords. 1990. *Silvics of North America: Vol. 1. Conifers*. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC. Available from http://na.fs.fed.us/spfo/pubs/silvics_manual/Volume_1/picea/glauca.htm [accessed 23 April 2014].

Hungerford, R.D. 1986. Vegetation response to stand cultural operations on small stem lodgepole pine stands in Montana. In: *Weed control for forest productivity in the interior West*; 1985 February 5-7; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension. pp. 63-71.

Klinka, K., R.E. Carter, M.C. Feller, and Q. Wang. 1989. Relations between site index, salal, plant-communities, and sites in coastal douglas-fir ecosystems. *Northwest Sci.* 63(1): 19-28. Available from http://www.vetmed.wsu.edu/org_nws/NWSci%20journal%20articles/1989%20files/Issue%201/v63%20p19%20Klinks%20et%20al.PDF [accessed 4 August 2014].

Lieffers, V.J., and K.J. Stadt. 1994. Growth of understory *Picea glauca*, *Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstory light transmission. *Can. J. For. Res.* 24(6): 1193-1198. doi:10.1139/x94-157.

Man, C.D., P.G. Comeau, and D.G. Pitt. 2008. Competitive effects of woody and herbaceous vegetation in a young boreal mixedwood stand. *Can. J. For. Res.* (7): 1817–1828. doi:10.1139/X08-032.

Matsushima, M., and S.X. Chang. 2006. Vector analysis of understory competition, N fertilization, and litter layer removal effects on white spruce growth and nutrition in a 13-year-old plantation. *For. Ecol. and Manage.* 236(2-3): 332–341. doi:10.1016/j.foreco.2006.09.018.

McCloskey, J.W. 1998. Soil Survey of Haines Area, Alaska. United States Department of Agriculture, Natural Resources Conservation Service, in cooperation with the University of Alaska Fairbanks Agricultural and Forestry Experiment Station, and the State of Alaska Department of Natural Resources. Available from <http://soildatamart.nrcs.usda.gov/Manuscripts/AK641/0/Haines.pdf> [accessed 9 May 2013].

Messier, C., and J.P. Kimmins. 1991. Above- and below-ground vegetation recovery in recently clearcut and burned sites dominated by *Gaultheria shallon* in coastal British Columbia. *For. Ecol. Manage.* 46(3-4): 275-294. doi:10.1016/0378-1127(91)90236-O.

Moss, E.H. 1936. The ecology of *Epilobium angustifolium* with particular reference to rings of periderm in the wood. *Am. J. of Bot.* 23(2): 114-120. doi:10.2307/2436304.

Nams, V.O., N.F.G. Folkard, and J.N.M. Smith. 1993. Effects of nitrogen fertilization on several woody and nonwoody boreal forest species. *Can. J. of Bot.* 71(1): 93–97. doi:10.1139/b93-011.

Nienstaedt, H., and J.C. Zasada. 1990. *Picea glauca* (Moench) Voss White Spruce. In Burns, Russell M., and Barbara H. Honkala, tech. coords. 1990. *Silvics of North America: Vol. 1. Conifers. Agriculture Handbook 654.* U.S. Department of Agriculture, Forest Service, Washington, DC. Available from http://na.fs.fed.us/spfo/pubs/silvics_manual/Volume_1/picea/glauca.htm [accessed 23 April 2014].

Phipps, H.M. 1977. White Spruce seedlings respond to density and fertilizer treatments in a plastic greenhouse. Research Note NOR-18. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 28(1):8-10,38. Available from http://www.rngr.net/publications/tpn/28-1/28_1_8_10.pdf [accessed 23 April 2014].

Rygiewicz, P.T., C.S. Bledsoe, and R.J. Zasoski. 1984. Effects of ectomycorrhizal and solution pH on [¹⁵N] ammonium uptake by coniferous seedlings. *Can. J. For. Res.* 14(6): 885–892. doi:10.1139/x84-158.

Schofield, J.J. 1993. *Alaska's wild plants: A guide to Alaska's edible harvest.* Alaska Northwest Books, Portland, Oregon. pp. 63.

Shropshire, C., R.G. Wagner, F.W. Bell, and C. J. Swanton. 2001. Light attenuation by early successional plants of the boreal forest. *Can. J. For. Res.* 31(5): 812–823. doi:10.1139/cjfr-31-5812.

Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Official Soil Series Descriptions. Available Online. Accessed [February/10/2008].

Staples, T.E., K.C.J. Van Rees, and C. van Kessel. 1999. Nitrogen competition using N-15 between early successional plants and planted white spruce seedlings. *Can. J. For. Res.* 29(8): 1282–1289. doi:10.1139/cjfr-29-8-1282.

Sterck, F., M. Martínéz-Ramos, G. Dyer-Leal, J. Rodríguez-Velazquez, and L. Poorter. 2003. The consequences of crown traits for the growth and survival of tree saplings in a Mexican lowland rainforest. *Functional Ecology*. 17(2): 194–200. doi:10.1046/j.1365-2435.2003.00729.x.

Van Cleve, K., and J.C. Zasada. 1976. Response of 70-year-old white spruce to thinning and fertilization in interior Alaska. *Can. J. For. Res.* 6(2): 145-152. doi:10.1139/x76-018.

Valentine, D.W., and H.L. Allen. 1990. Foliar responses to fertilization identify nutrient limitation in loblolly pine. *Can. J. For. Res.* 20(2): 144-151. doi:10.1139/x90-020.

Wagner, R.G., and A.P. Robinson. 2006. Critical period of interspecific competition for four northern conifers : 10-year growth response and associated vegetation dynamics. *Can. J. For. Res.* 36(10): 2474–2485. doi:10.1139/X06-058.